

GROWTH AND REPRODUCTION OF THE EASTERN SPINNER DOLPHIN,
A GEOGRAPHICAL FORM OF *STENELLA LONGIROSTRIS*
IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

Estimates of life history parameters for use in assessing status of the population of the eastern spinner dolphin and assessing impact of incidental mortality in the yellowfin tuna fishery are developed from data on 2,675 specimens collected from 1968 to 1975. Average length at birth is 77.0 cm, gestation is 10.6 mo, average length at 1 yr is approximately 134 cm. Three alternative hypotheses of rate of deposition of dentinal growth layers are: I) 1.5 layers/yr throughout life; II) 1.5 layers in the first year, 1/yr thereafter (most favored hypothesis); and III) 1.5 layers until puberty (at 5.5 layers in females and 9 layers in males), and 1 yr thereafter. Males attain sexual maturity on the average at about 170 cm (range 160–195) and 9–12 layers (6.0–11.5 yr), depending on the criterion of testis–epididymis weight chosen. Average length at attainment of social maturity is unknown. Average length of adult males is 174–176 cm. Females on the average attain sexual maturity at 165 cm (5.5 layers or 3.7, 5.0, or 3.7 yr under Hypotheses I, II, and III). Average length of sexually adult females is 171 cm (range 152–187). Ovulation rate is 1/growth layer (1/0.67–1.00 yr) until about 10 ovarian corpora have been accumulated, after which the rate declines. Approximately 1% of adult females are postreproductive. Best estimates of annual pregnancy rate range from 0.450 (based on 1973 data) to 0.474 (based on 1974 data). The pooled estimate for all years' data is 0.461. The corresponding estimates of calving interval (reciprocal of pregnancy rate) are 2.22 yr, 2.11 yr, and 2.17 yr, respectively. Pregnancy rate decreases after age of about 12 layers (8.0, 11.5, or 10.2 yr) concomitant with increase in lactation rate. Overall sex ratio is near parity, but there are about 6% more females than males in adults. Best estimates of gross annual reproductive rate based on the 1973, 1974, and 1975 data are 0.099, 0.103, and 0.105, respectively. The estimate based on pooled data for the 3 yr is 0.102. The estimates are compared with estimates for the spotted dolphin, *Stenella attenuata*, and for other cetaceans.

This paper presents the results of a study of the life history of the eastern spinner dolphin, a geographical form² of *Stenella longirostris* (Gray 1828), in the eastern tropical Pacific. The eastern spinner dolphin accounted for the second-highest level of incidental mortality in the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific through 1975, after the offshore spotted dolphin, a form of *S. attenuata* (Gray 1846) (Perrin 1969, 1975a; Perrin et al.³) The purpose of the

study was to develop estimates of life history parameters for use in assessing the status of the eastern spinner dolphin stock and the impact on the stock of incidental mortality in the yellowfin tuna fishery. Preliminary results of partially completed analyses reported here in full appeared in Perrin et al.⁴

Very little previously published information is available on growth and reproduction of the pantropically distributed *S. longirostris*. Cadenat and Doure (1959) listed body weights and gonadal

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²Perrin (1975b) gave the eastern spinner dolphin subspecific rank but stated that the nomenclature is not yet resolved, because the holotype of the species is from an unknown locality. The term "geographical form" is used here as a substitute for the more unwieldy "[*Stenella longirostris*] subspecies (unnamed)." The term "dolphin" is used in conformance with the "list of smaller cetaceans recognized" adopted by the Subcommittee on Smaller Cetaceans, Scientific Committee, International Whaling Commission (Anonymous 1975).

³Perrin, W. F., T. D. Smith, and G. T. Sakagawa. 1974. Status of populations of spotted dolphin, *Stenella attenuata*, and spinner dolphin, *Stenella longirostris*, in the eastern tropical Pacific.

Working Document for Meeting of Ad Hoc Consultants Group on Small Cetaceans and Sirenians (Ad Hoc Group 2), Working Party on Marine Mammals, Advisory Committee of Experts on Marine Resources Research (ACMRR) of the Food and Agriculture Organization of the United Nations, La Jolla, Calif., December 16–19, 1974. SWFC Admin. Rep. LJ-74-42, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 22 p. (Unpubl. rep.)

⁴Perrin, W. F., D. B. Holts, and R. B. Miller. 1975. Preliminary estimates of some parameters of growth and reproduction of the eastern spinner porpoise, *Stenella longirostris* subspecies. SWFC Admin. Rep. LJ-75-66, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 33 p. (Unpubl. rep.)

data for two males (1,940 and 2,040 mm) and two females (1,790 and 1,800 mm) from off Senegal in the tropical Atlantic. Layne (1965) published similar data for two males (1,845 and 1,910 mm) and one female (1,965 mm) from Florida. Pilson and Waller (1970) reported on an adult female of *S. microps* [= *S. longirostris*] 176 cm long, from the eastern Pacific. Harrison et al. (1972) published detailed length, weight, and gonadal data for 12 males (79 to 185 cm) and 21 females (86 to 188 cm) of *S. longirostris* from the eastern Pacific; five males (150 to 182 cm) and two females (169 and 179 cm) of *S. roseiventris* [= *S. longirostris*] from Hawaii; and nine specimens from the eastern Pacific, eight males (165 to 178 cm), and one female (171.5 cm) listed as "probably *S. longirostris*." In their discussion of growth and reproduction, however, they did not differentiate between *S. longirostris* and *S. graffmani* [= *S. attenuata*], a larger species that differs significantly from *S. longirostris* in several features of life history (compare results below with those for *S. attenuata* in Perrin et al. (1976) and Kasuya et al. (1974)).

Several recent reports emanating from the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, have dealt with the developmental components of various aspects of the life history of *S. longirostris* other than reproduction. Perrin (1972) described the development of the color pattern in eastern Pacific forms of the species. Perrin and Roberts (1972) analyzed changes in organ weights with size, based on 14 specimens. Dailey and Perrin (1973) described differences in parasite frequencies correlated with age in 19 specimens. Perrin (1975a, b) described developmental variation in morphology in the eastern Pacific and defined three geographical forms (subspecies), of differing adult size: the less-than-2-m-long "eastern spinner," the subject of this report; the slightly larger "whitebelly spinner," found farther offshore; and the "Costa Rican spinner," which is restricted to the coastal waters of Central America and attains a total length of well over 2 m.

This paper treats only the eastern spinner, the form of *S. longirostris* most heavily involved in the tuna fishery through 1975 in terms of numbers of seine net sets and numbers killed (Perrin 1975a). Some data for the whitebelly spinner are included in certain of the analyses of the eastern spinner, including those of length at birth and of brain weight relative to body length, for reasons explained below. A preliminary report on the white-

belly form of *S. longirostris* appeared in Perrin et al.⁵

METHODS AND MATERIALS

The Field Program

Nearly all of the data were collected by NMFS scientific observers aboard commercial tuna vessels. The data collection procedures were the same as previously described for the spotted dolphin (Perrin et al. 1976). Data on *S. longirostris* were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, and 30 in 1975. Some specimens were also collected in 1970 by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

The Sample

In 1971 and early 1972, when the observer program was very limited, adult female specimens were selected for dissection when available, and the samples for those periods are, therefore, biased with regard to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was practiced in determining which animals were to be examined, and those samples are assumed to be cross-sectional with respect to the kill. Fetuses were not collected in 1968.

The sample of animals for which life history data including at least, but not restricted to, sex and body length includes 2,675 specimens, 2,663 from precisely known localities (Figure 1) and 12 from imprecisely known localities, from the eastern tropical Pacific between lat. 21°N and 3°S and west to long. 117°W. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1). Length-frequency distributions by 5-cm increments for males and females, including fetuses, are presented by year and month in Figures 2 and 3.

⁵Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Preliminary estimates of some parameters of growth and reproduction of the whitebelly spinner dolphin, a geographical form of *Stenella longirostris*, in the eastern tropical Pacific. Working document submitted to Meeting of Subcommittee on Small Cetaceans, Scientific Committee, International Whaling Commission, London, 7-8 June 1976. SWFC Admin. Rep. LJ-76-12, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 36 p. (Unpubl. rep.)

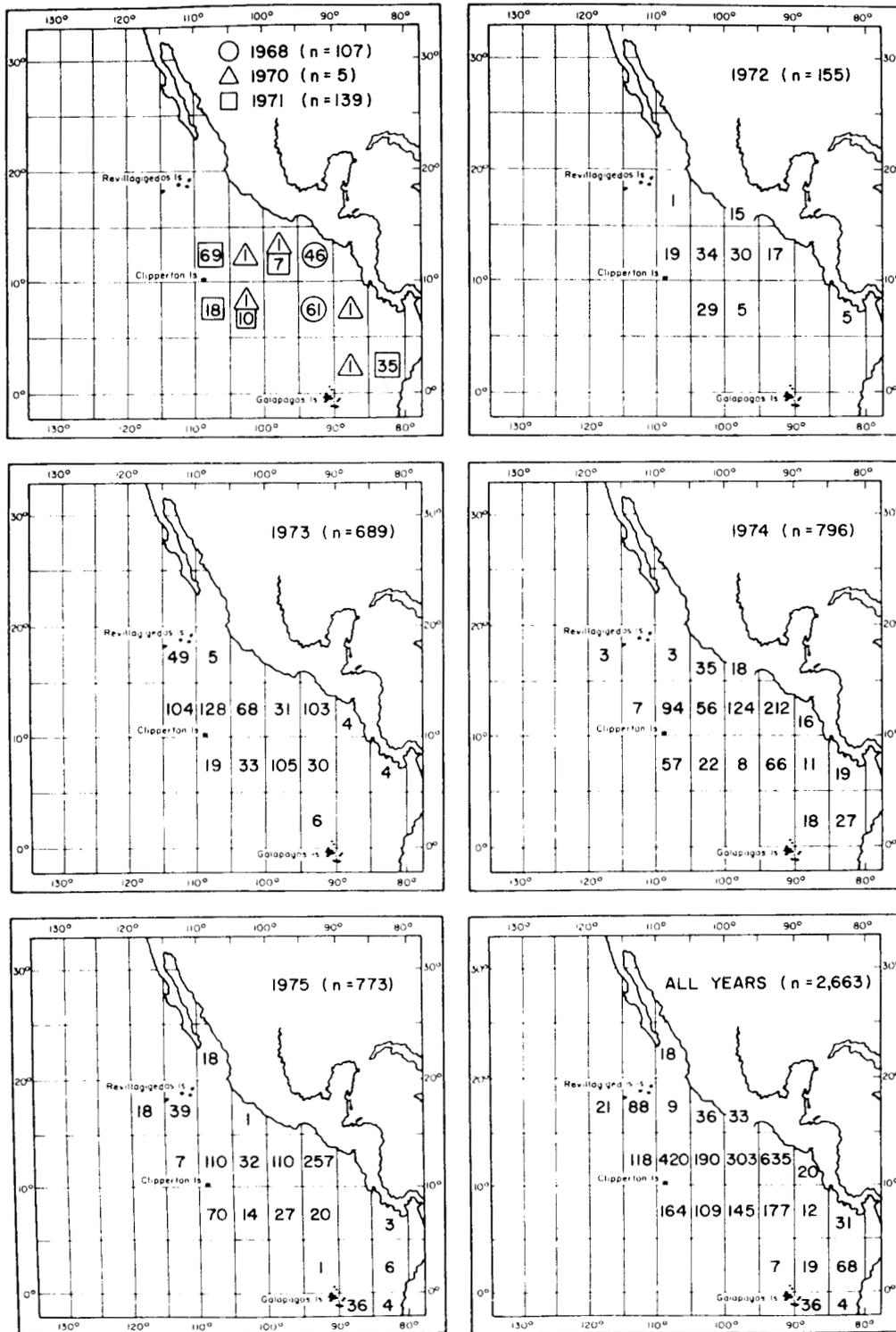


FIGURE 1.—Samples of *Stenella longirostris* collected 1968-75, by 5° square.

TABLE 1.—The sample of eastern spinner dolphins used in the life history analysis, by year and month.

Month ²	1968		1970		1971 ¹		1972 ¹		1973		1974		1975		All years		Total
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	
Jan.			1	2	2	11	9	12	23	24	85	104	163	170	283	323	606
Feb.					20	15		15	135	128	230	209	68	72	453	439	892
Mar.							11	35	79	78	26	18	32	31	148	162	310
Apr.	52	55					25	15	50	53	41	30	9	25	177	178	355
May							6	12	1	7	1	3	16	13	24	35	59
June												3	19	21	19	24	43
July			2										16	25	18	25	43
Aug.											3	1	12	12	15	13	28
Oct.							10	7	7	7			17	33	34	47	81
Nov.					35	39			49	45	19	27	12	9	115	120	235
Dec.					6	11			3	3					9	14	23
Total	52	55	3	2	63	76	61	96	347	345	405	395	364	411	1,295	1,380	2,675

¹In these years, adults were selected (except in Oct. 1972). Fetuses were not collected in 1968.

²No samples in September.

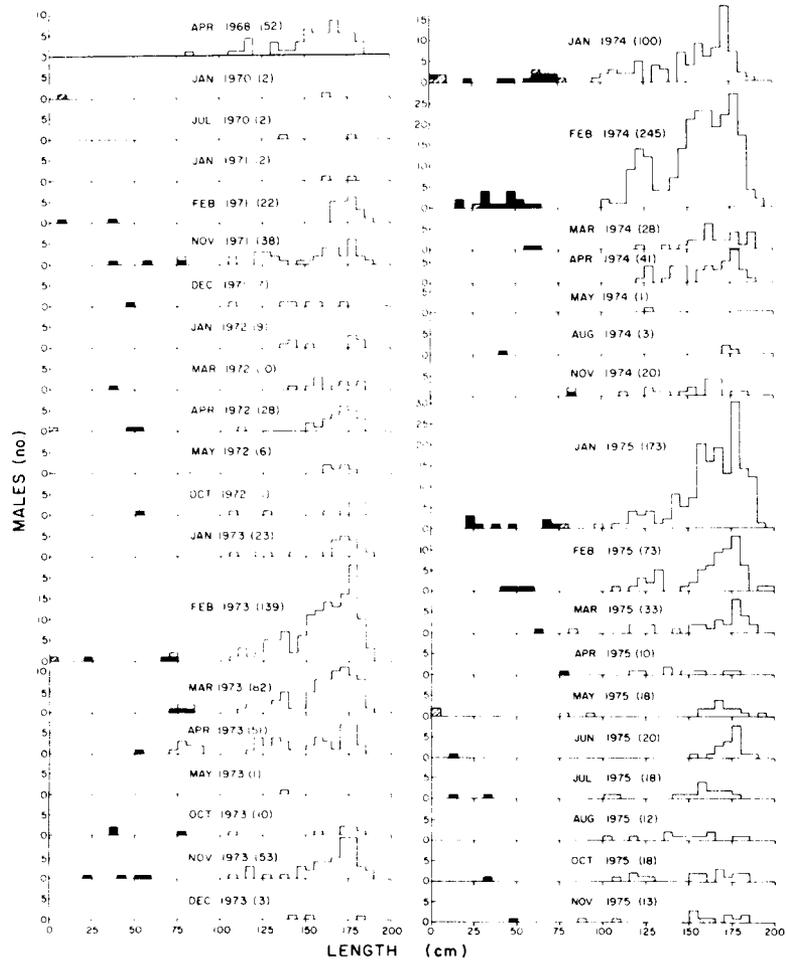


FIGURE 2.—Length-frequency distribution, by 5-cm increments, of collected male eastern spinner dolphins by year and month. Shaded squares are fetuses. Hatched squares are small fetuses of unknown sex (plotted with the males). Sample sizes in parentheses.

Laboratory Procedures

Most laboratory procedures were the same as reported for the earlier study of the growth and reproduction of the spotted dolphin (Perrin et al.

1976). The techniques used in sectioning and reading, however, differed somewhat. Some of the approximately 2,500 teeth prepared (includes recuts, multiple specimens, etc.) were sectioned with multiple cuts, using a high-speed diamond saw

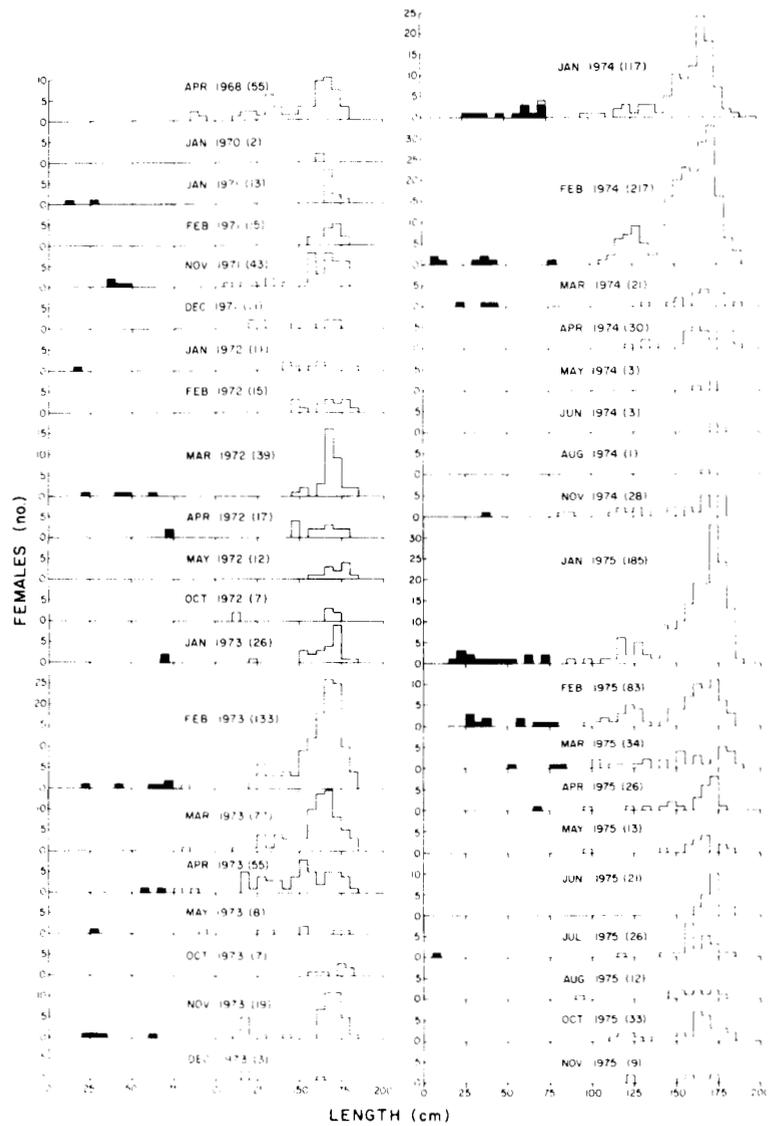


FIGURE 3.—Length-frequency distributions, by 5-cm increments, of collected female eastern spinner dolphins by year and month. Shaded squares are fetuses. Sample sizes in parentheses.

(Felker⁶ model 80BQ Hi-speed Precision Cut-off Machine—36,000 rpm) with a single blade, as for *S. attenuata* (Perrin et al. 1976), but most were sectioned with a single cut of tandem blades (yielding a section of uniform 10/1,000-in thickness) with a low speed saw (Isomet model 11-1180 low speed saw—speed variable to 300 rpm). The latter method yielded sections of more uniform thickness and with fewer extraneous surface striations than did the former. After cutting, sections were im-

⁶Reference to trade names does not imply endorsement of the product by the National Marine Fisheries Service, NOAA.

mediately mounted under coverslips on microscope slides in balsam, omitting the clearing step used for the *S. attenuata* teeth. Our reading and scoring methods also differed from those in the earlier study. We found postnatal dental growth to be much more consistent in *S. longirostris* than in *S. attenuata* in pattern of deposition and in readability. No teeth were encountered that did not contain an open cavity, albeit in older specimens a very small one, and a smaller proportion of teeth from younger animals (<12 to 13 layers) contained convoluted secondary dentine than in *S. attenuata*. In the study of *S. attenuata*, growth

layers were merely counted to the nearest half layer. In view of the better readability of the *S. longirostris* material, we felt that the approach could be refined. We measured the thickness of each growth layer on an image projected on a 16-cm diameter ground-glass screen attached to a compound microscope using dial calipers accurate to 0.1 mm. The total magnification on the screen was approximately 263 diameters. The first two layers inside the neonatal tooth were measured at approximately the same point along the length for each tooth, about halfway between the proximal end of the neonatal tooth (point where neonatal line meets outer surface) and the distal end of the neonatal pulp cavity. Layers beyond the second were measured at the place along the length of the tooth where they were most clearly defined. In converting measurements to layer units, non-innermost layers beyond the first layer were scored as full layer units regardless of thickness. The first layer, second (when innermost), and subsequent layers (when innermost) were treated differently, as follows:

First Layer

Cumulative percent of 417 first layers measured rapidly approaches an asymptote at approximately 0.20 mm (Figure 4). A first layer 0.20 mm thick or thicker was therefore scored as a full layer unit, and the thickness of a first layer <0.20 mm thick was divided by 0.20 mm to yield a partial layer unit.

Second Layer

In 361 teeth with three or more layers, the second layer averaged 0.145 mm thick with relatively low variance (Figure 5). In teeth with two layers, the second layer was scored as a full layer unit if 0.145 mm thick or thicker. An innermost second layer <0.145 mm thick was scored as a partial layer unit by division of the thickness by 0.145 mm.

Layers Beyond Second Layer

Full layers beyond the second layer averaged more than 95% of the thickness of the next older, adjacent layer, with considerable variation that increased toward the center of the tooth (Figure 6). We assumed, as a reasonable approximation, that complete layers beyond the third are of about the

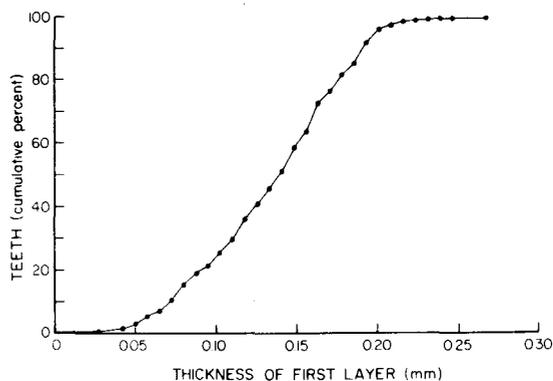


FIGURE 4.—Cumulative percent of first growth layers in relation to thickness of layer in the teeth of 417 eastern spinner dolphins showing asymptote of sigmoid curve at about 0.20 mm.

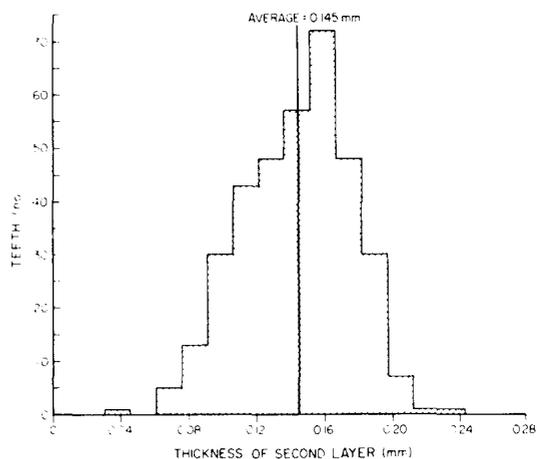


FIGURE 5.—Frequency distribution of thickness of second growth layer in teeth of 361 eastern spinner dolphins.

same thickness as adjacent layers, and thickness of the innermost layer in teeth with three or more layers was scored as a proportion of the next older, adjacent layer. Layer scores thus obtained were added and rounded off to the nearest tenth of a layer.

Brain weights were obtained from brains dissected out of freshly thawed heads or whole carcasses of specimens deep frozen at sea aboard tunaboats, except for nine weights for *S. attenuata* (two fetuses, two neonates, and four adults) obtained from George A. Sacher (Argonne National Laboratory, Argonne, Ill., pers. commun.).

Testes were weighed with the epididymes attached.

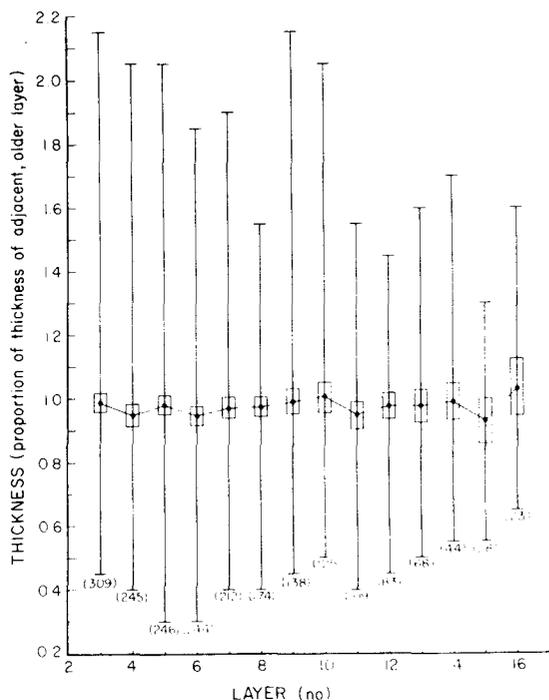


FIGURE 6.—Thickness of growth layers, beyond second postnatal layer, in teeth of the eastern spinner dolphin as proportion of thickness of next older, adjacent zone. Box is one SD on each side of mean; vertical line is range; sample size in parentheses.

RESULTS

Growth

Length at Birth

The largest fetus encountered was 84 cm long. The smallest free-swimming calf was 70 cm long. Estimated average length at birth is 76.9 cm. The estimate is based on a weighted linear regression of percent postnatal on body length, for 3-cm groupings, of 101 specimens (54 fetuses and 47 neonates) between 67 and 99 cm long (Figure 7) collected in random samples. Because of the small sizes of the available samples, 23 specimens of the whitebelly form (11 neonates and 12 fetuses) and 23 specimens unidentified to geographical form (16 neonates and 7 fetuses) were included. This is justified because of the small difference in length of adults of the two forms (≈ 5 cm—Perrin 1975a). Such a difference could be expected to translate into a probable error in the estimate of length at birth, based on the present sample composition, of

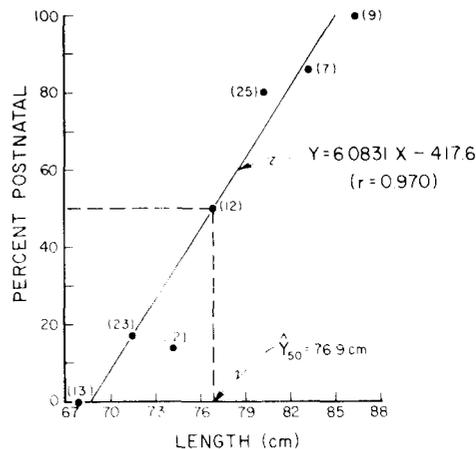


FIGURE 7.—Estimation of average length at birth, based on weighted linear regression of percent postnatal on body length, in 3-cm increments, for 101 specimens of *Stenella longirostris* (54 fetuses and 47 neonates) between 67 and 88 cm long.

≈ 0.5 cm, less than that to be expected to be introduced by reduction of the sample size (by 47%) through restriction to specimens known to be eastern spinner dolphins. The estimate is rounded off to 77 cm in analyses below.

This method of estimating average length at birth assumes that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. It also assumes equal rates of prenatal and postnatal natural mortality and assumes that the stresses imposed by pursuit and capture do not cause premature births during the chase or in the net. It was not possible to test these assumptions although some evidence indicates that the last may not be justified (see discussion below in The Calving Cycle and Pregnancy Rate).

Length of Gestation and Fetal Growth

The usual method used to estimate length of gestation is that of Laws (1959), in which progression of a mode in fetal lengths is followed through the seasons. This method was used to estimate length of gestation for the spotted dolphin (Perrin et al. 1976). The method could not be applied to the present samples of data for the eastern spinner dolphin, however. Although breeding is perhaps synchronous at some level (e.g., note peaks in the length-frequency distributions for postnatal males and females in February and April 1973, and February 1974—Figures 2, 3), progression of

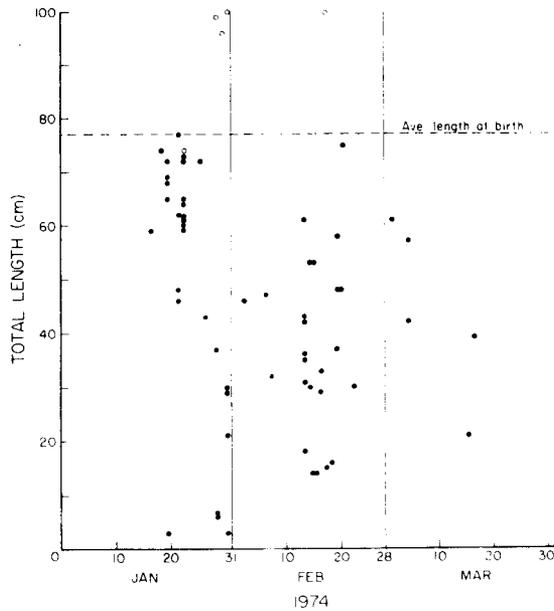


FIGURE 8.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-March 1974.

fetal modes is not apparent in the data. For example, in the large samples of fetuses collected in January–March 1974 (Figure 8), a sharp mode at 60 to 75 cm in January is not apparent in February, even as neonates, and the diffuse mode at 30 to 60 cm in February is not accounted for in the January sample. A probable reason for these discrepancies is the existence of area-related differences in the timing of calving peaks or in the degree of synchrony of breeding. The tuna fleet, our source of samples, moves around from month to month. The January 1974 samples came for the most part from more easterly, offshore localities than did the February samples (Figure 9). In other words, in 1974, calving in the more offshore region may have been sharply synchronized, with a peak in February–March, while in the more onshore region, calving may have been spread over most of the year. This hypothesis is reinforced by the data for January–April 1975, when sizeable samples of fetuses were collected in the more onshore region during both January and February and smaller samples through April (Figure 10) were from more offshore (around Clipperton Island), northerly

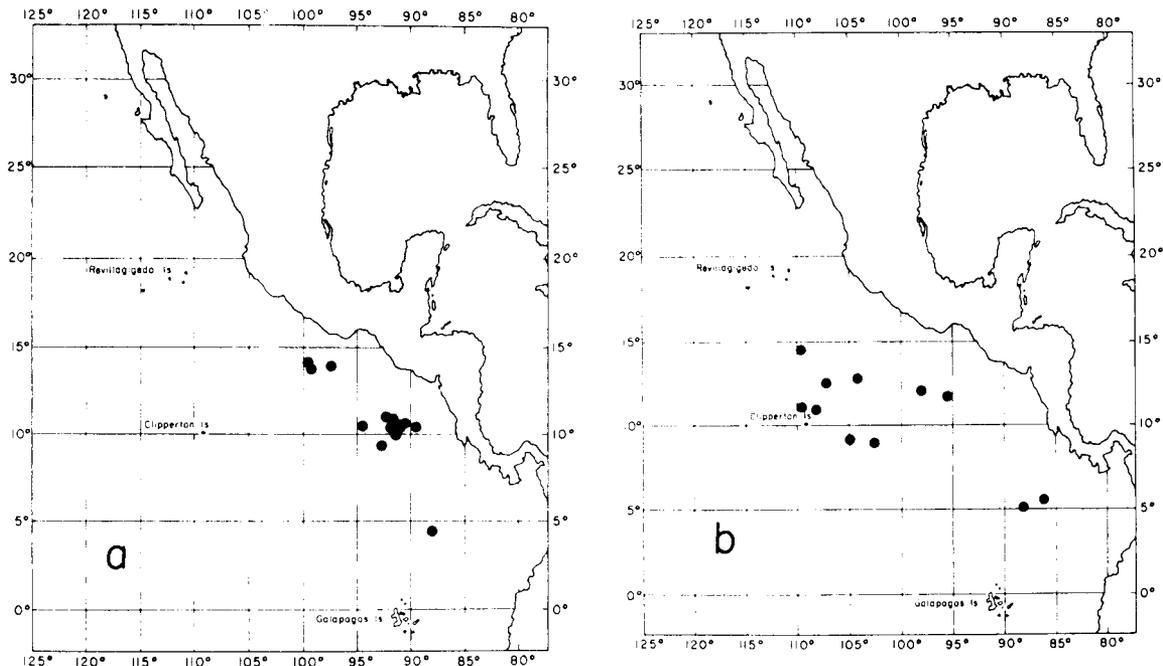


FIGURE 9.—Localities at which fetuses of the eastern spinner dolphin were collected in January (a) and February (b) 1974.

(Revillagigedo Islands), or southerly (near the Equator, east of the Galapagos Islands) regions. Even if only onshore samples are considered (those circled in Figure 10), there is no clear pattern of progression of fetal length modes (Figure 11). It is, of course, possible that the size of the population unit within which breeding is synchronous may be smaller than suggested by the onshore-offshore comparison. In any case, this complexity makes impossible the use of Laws' method for estimating gestation based on aggregated samples, and stratification of the data to even smaller areas than used above yields samples too small for meaningful analysis. For these reasons, we attempted to estimate length of gestation by two other, less

direct methods: a) on the basis of relative length at birth compared with that of other, closely related delphinids for which estimates of gestation period exist, and b) on the basis of a recently discovered empirical relationship between brain size parameters and gestation in mammals.

ESTIMATE FROM COMPARISON WITH OTHER DELPHINIDS BASED ON LENGTH AT BIRTH.—Estimates of length of gestation derived by comparable methods are available for four delphinids, *sensu stricto* (Table 2). There is a positive correlation among these closely related forms between length of gestation and length at birth (Figure 12). Extrapolation of this relationship to

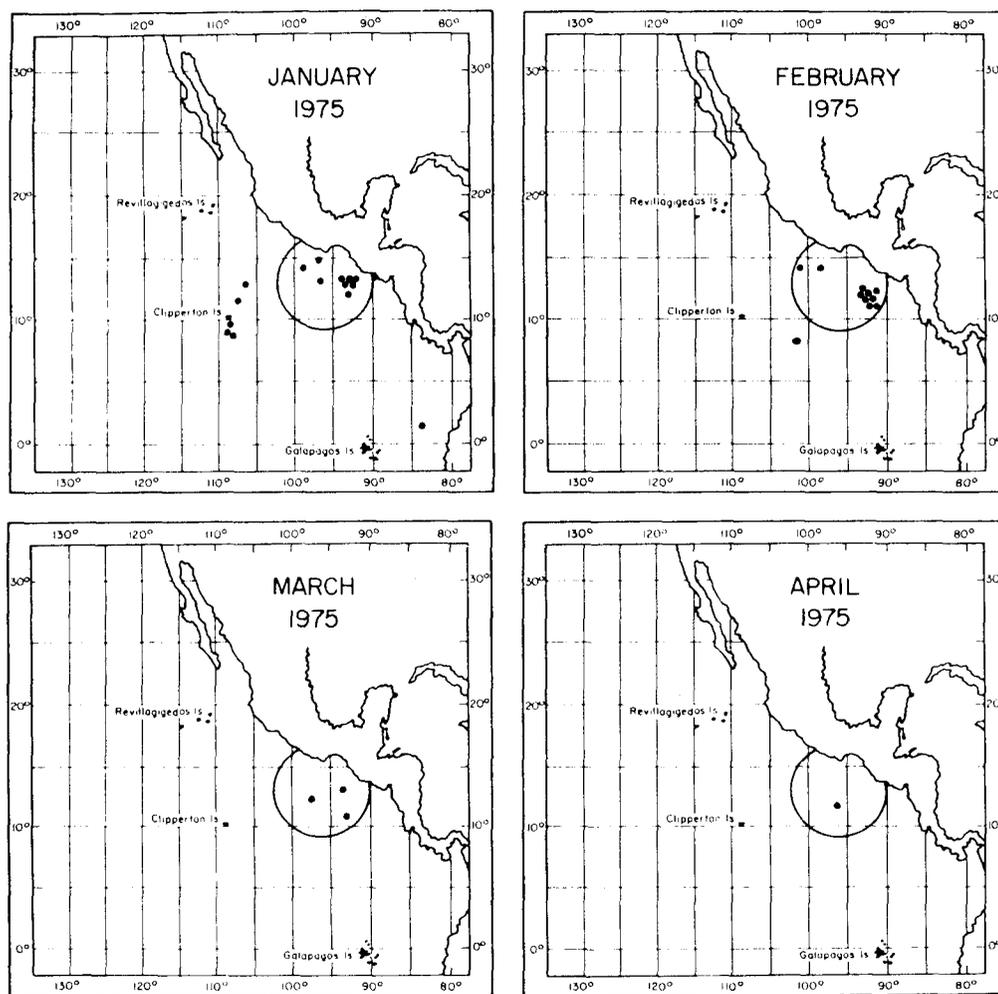


FIGURE 10.—Localities at which fetuses of the eastern spinner dolphin were collected, January-April 1975.

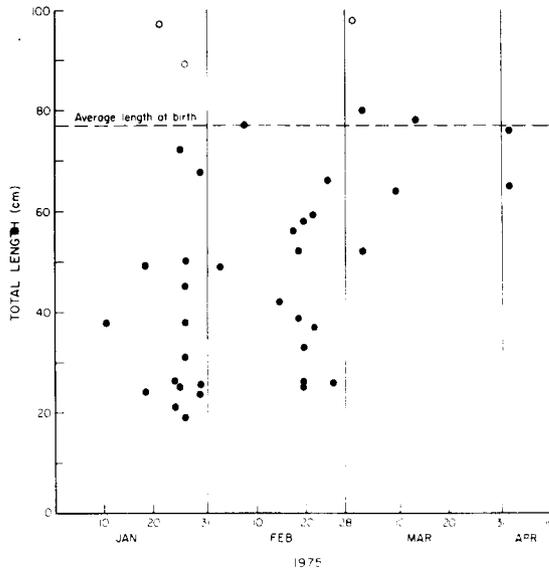


FIGURE 11.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-April 1975 (specimens from localities circled in Figure 10).

TABLE 2.—Estimated average length at birth and length of gestation in four delphinids. Data for *Globicephala* from Sergeant (1962), for *Tursiops* from Sergeant et al. (1973), for *Stenella coeruleoalba* from Kasuya (1972), for *S. attenuata* from Kasuya et al. (1974) (off Japan) and from Perrin et al. (1976) (eastern Pacific). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975).

Species	Length at birth (cm)	Gestation (mo)
Long-finned pilot whale <i>Globicephala melaleuca</i> (Newfoundland)	176.0 (average of males and females)	15.75 (15.5-16.0)
Bottlenose dolphin <i>Tursiops truncatus</i> (northeast Florida)	100.0	12.0
Striped dolphin <i>Stenella coeruleoalba</i> (off Japan)	99.8	12.0
Spotted dolphin <i>Stenella attenuata</i> a. (off Japan) b. (eastern Pacific)	89.0 82.5	11.2 11.5

length at birth for *S. longirostris* of 77 cm yields a deduced length of gestation of 10.74 mo (325 days).

ESTIMATE BASED ON GROWTH PARAMETERS OF THE BRAIN.—Sacher and Staffeldt (1974) recently demonstrated an empirical relationship between gestation time and brain weight in placental mammals. This relationship explains more of the wide variation in mammalian gestation times than do previous empirical approaches involving body size parameters, such as cube root

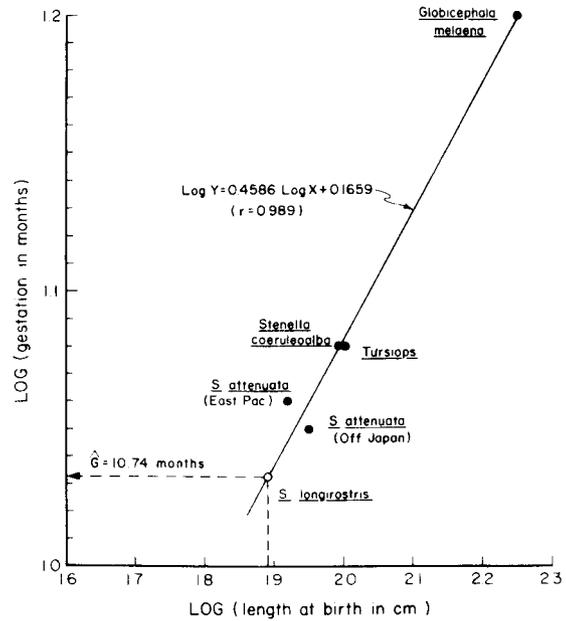


FIGURE 12.—Relationship between log of length of gestation and log of length at birth in four delphinid cetaceans, with extrapolation to predicted length of gestation in the eastern spinner dolphin.

of weight at birth (Huggett and Widdas 1951) or length at birth (as in above estimate). They developed a predictive equation based on linear multiple regression analysis:

$$\log G = 0.274 \log E_n + 0.144 \log A_e + 0.173 \log N + 1.853$$

where G = gestation time in days
 E_n = neonatal brain weight in grams
 A_e = "brain size advancement," or ratio of neonatal to adult brain weight
 N = litter size (1 in cetaceans).

Application of this equation to brain data for *S. longirostris* (Figure 13—neonatal brain weight = 231 g, adult brain weight = 465 g) yields an estimate of gestation time of 286 days (9.45 mo). The method has not yet been tested on a significant number of delphinid species for which gestation time has been more directly estimated,⁷ and we

⁷The estimates used by Sacher and Staffeldt of brain weight at birth and adulthood for *Tursiops* are from Lilly (1967) and are based on samples of unstated and probably small size, a very important consideration in light of the large individual variation in these features (Figures 15, 16) and geographical variation in overall size (Anonymous 1975). For example, eight *Tursiops* brain weights summarized by Gahr and Pilleri (1969) averaged

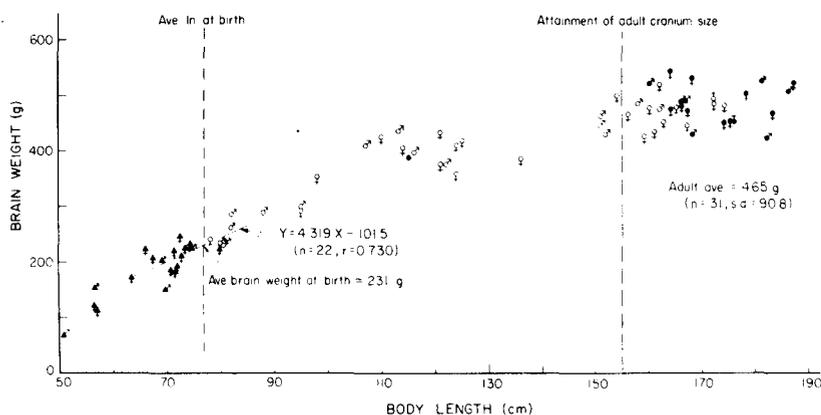


FIGURE 13.—Scatterplot of brain weight on body length for 77 specimens of *Stenella longirostris* from the eastern Pacific. The sample of fetuses and neonates (< 100 cm) includes 11 eastern spinner dolphins, 9 whitebelly spinner dolphins, and 9 specimens (mostly fetuses) unidentified to race. Triangles are fetuses, open circles are sexually immature postnatal specimens, shaded circles are sexually adult specimens (by criteria explained in text below). Length at attainment of adult cranium size based on data in Perrin (1975b). The linear regression to estimate brain weight at birth is based on 22 near-term fetuses and neonates 63 to 88 cm long.

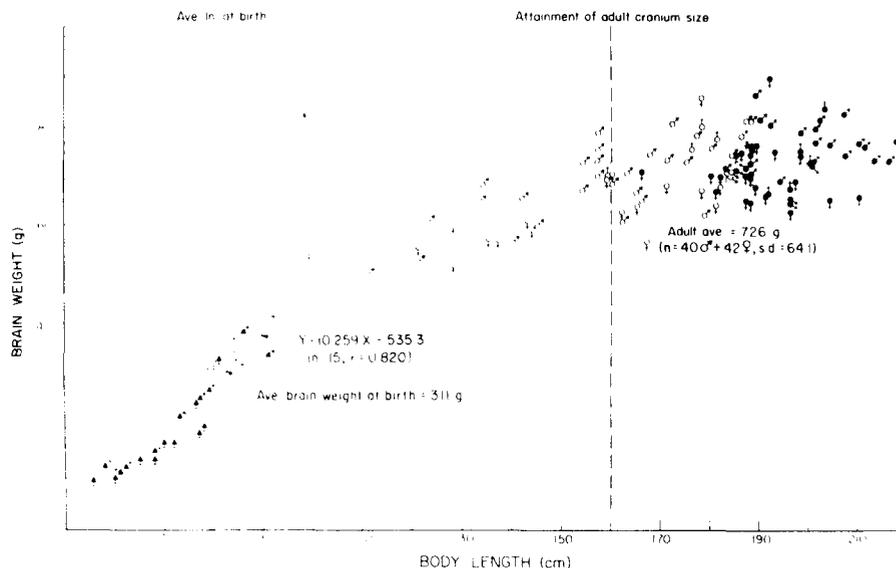


FIGURE 14.—Scatterplot of brain weight on body length for 133 eastern spinner dolphins from the offshore eastern tropical Pacific. Triangles are fetuses, open circles are sexually adult specimens. Linear regression to estimate brain weight at birth based on near-term fetuses and neonates, 73 to 91 cm long. Criteria for sexual maturity and basis for length at attainment of adult cranium size from Perrin (1975b).

1,475 g, compared with the 1,600 g reported by Lilly based on an unknown sample size. Twelve nonneonatal brain weights (probably including some of juveniles) published by Morgane and Jacobs (1972) ranged from 1,260 to 1,950 g and averaged 1,536 g. Thus, deviation of the estimate of Sacher and Staffeldt for *Tursiops* (396 days, or 13.08 mo) from the more directly obtained estimate of 12 mo (Sergeant et al. 1973), an overestimate of about 10%, is of unknown significance and probably reflects statistical error as well as possibly deductive error.

therefore applied the equation to brain data for the spotted dolphin, *S. attenuata* (Figure 14— neonatal brain weight = 311 g, adult brain weight = 726 g). The estimate of gestation time obtained is 304 days, or 10.03 mo, as compared with 11.5 mo (rounded off) estimated by a more direct method

(Perrin et al. 1976). If it be assumed that some factor in delphinid growth is unaccounted for in the Sacher-Staffeldt model and that gestation time for *S. longirostris* is underestimated to a similar degree (11.5 mo minus 10.0 mo/11.5 mo, or 13%), an adjusted Sacher-Staffeldt estimate of 10.54 mo is obtained.

The estimate based on length at birth (10.74 mo) and the adjusted Sacher-Staffeldt estimate (10.54 mo) are close to each other, and a rounded off average of the two estimates, 10.6 mo, is used below in the analyses of reproduction. Making the assumption that fetal growth follows a pattern similar to that in *S. attenuata*, i.e., that t_0 in Laws' fetal growth equation $L = a(t - t_0)$ is approximately the same proportion of gestation time as in *S. attenuata*, or $0.135 t_g$ (Perrin et al. 1976), a fetal growth curve can be estimated (Figure 15). The slope of the linear portion of the curve is 8.367 cm/mo, as compared with 8.283 cm/mo estimated for *S. attenuata* (Perrin et al. 1976).

Postnatal Growth

We found it impossible to estimate postnatal growth rates by the usual method of following the seasonal progression of length modes, for the reasons discussed above. We deduced an estimate of growth rate during the first 10 to 11 mo by application of the equation, $\log Y = 0.99 \log X - 1.33$, expressing an inferred relationship in toothed cetaceans between length at birth (X above) and the difference (Y above) between the growth rates during the linear phases of fetal and early postnatal growth (Perrin et al. 1976). The predicted difference based on length at birth of 77 cm is 3.60 cm/mo. Subtraction of this from the

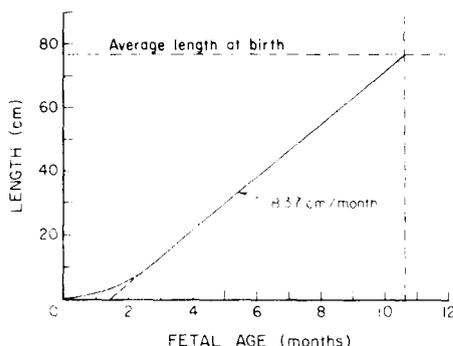


FIGURE 15.—Estimated fetal growth curve for the eastern spinner dolphin.

fetal linear growth (estimated above) of 8.37 cm/mo yields an estimate of average growth rate during the first 10 to 11 mo after birth of 4.77 cm/mo. If this is taken as an estimate of average growth rate during the first year, predicted length at 1 yr is 134 cm. This method overestimates length at 1 yr to some unknown, but slight extent, as growth is only approximately linear in the first year.

We examined the relationship between length and number of postnatal dentinal growth layers in the teeth for 183 males and 250 females (Figure 16). The occurrence in the samples of length-layer data for relatively more females than males with more than about 12 layers is accounted for by the fact that the sample of males selected for tooth-sectioning was stratified entirely by length, whereas the sample of females was stratified by length in juveniles and by number of ovarian corpora in adults. All females with more than 10 ovarian corpora were included in the sample, in addition to randomly selected, corpora-stratified subsamples of females with <10 corpora.

We fit growth curves to the data (to single-layer incremental means), using a two-cycle version of the Laird growth model (see Perrin et al. 1976 for discussion of the model). Juvenile males and females were considered jointly. The fit was forced through the origin (zero growth layers, and estimated length at birth of 77 cm), and asymptotic length (L_{∞}) was estimated as the average length of animals with 13 or more layers (L_{∞} for 12 males = 179.46 cm and for 60 females = 170.91 cm), fixing the upper ends of the two curves of the second cycle. The simultaneous iterative fitting procedure arrived at 4.111 growth layers (rounded off to 4 below) as the age at which convergence of the three curves (estimated onset of a secondary growth spurt) yields the best fit (Figure 16). Estimated length at this age is 156.85 cm. The Laird/Gompertz model (Laird 1969) is

$$L(t) = L_0 \exp \left\{ \frac{a}{\alpha} \left[1 - \exp(-\alpha t) \right] \right\}$$

where L = length in centimeters

t = age

L_0 = length at age zero

a = specific rate of exponential growth

α = rate of decay of exponential growth.

A form of the model generalized to the present case of more than one cycle is

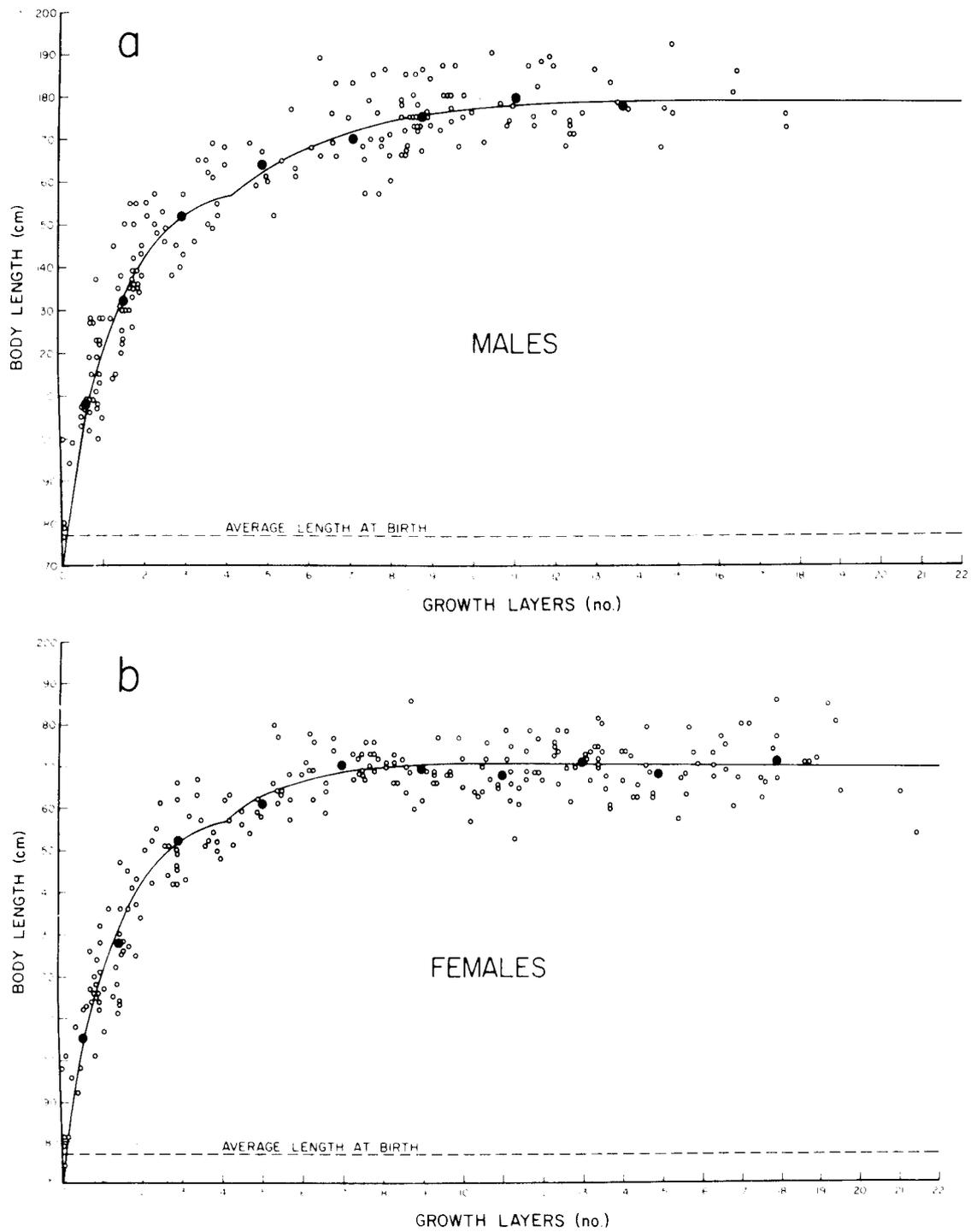


FIGURE 16.—Scatterplot of body length on number of postnatal dentinal growth layers in 183 male (a) and 250 female (b) eastern spinner dolphins. Circled dots are means for 0-1 layer, 1-2 layers, for 2-layer increments thereafter until 12 layers in males and 16 in females and for ≥ 12 layers and ≥ 16 layers, respectively. The line is a two-cycle Laird fit to single-layer incremental means (see text).

$$L(t) = L' \exp \left\{ \frac{a}{\alpha} \left[1 - \exp(-\alpha(t - t')) \right] \right\}$$

where L' = length (centimeters) at start of cycle
 t' = age (growth layers) at start of cycle.

The growth equation for juveniles of <4 growth layers is

$$L = 77 \exp \left\{ \frac{0.6630}{0.9098} \left[1 - \exp(-0.9098t) \right] \right\}.$$

The growth equation for males of >4 growth layers is

$$L = 156.85 \exp \left\{ \frac{0.0507}{0.3765} \left[1 - \exp(-0.3765(t - 4.11)) \right] \right\}.$$

and for females

$$L = 156.85 \exp \left\{ \frac{0.0546}{0.6354} \left[1 - \exp(-0.6354(t - 4.11)) \right] \right\}.$$

The fits of the model to both males and females is excellent, albeit slightly better for the females about the point of convergence of the two curves than for males.

The equations rearranged and reduced for estimating age from length are

δ and $\varphi < 157$ cm

$$t = -1.099 \ln(6.960 - 1.372 \ln L)$$

$\delta > 157$ cm

$$t = 4.113 - 2.656 \ln(38.540 - 7.426 \ln L)$$

$\varphi > 157$ cm

$$t = 4.113 - 1.574 \ln(59.871 - 11.645 \ln L).$$

Note: These equations should not be used to estimate age from actual length data except for grouped samples of smaller animals (about 165 cm or less in females and 170 cm in males), for which growth rate is still large compared with individual variation in length.

Estimated age in growth layers at 134 cm, the predicted length at 1 yr derived above from extrapolative comparison with other delphinids, is 1.57 layers. Since, as discussed above, the estimate of 134 cm is likely to be a slight overestimate due to some nonlinearity of growth during the first year, the estimate of 1.57 layers is rounded down (to the nearest half layer) to 1.5 layers for use

below in the various hypotheses of rate of accumulation of layers.

It appears that, effectively, in terms of the data yielded by the tooth readings, 1.5 layers are laid down in the first year. One possible explanation alternative to that of actual deposition of 1.5 layers/yr is that a single layer is laid down in the first year, but that in some individuals (about half) there is a strongly developed subsidiary line within the layer that makes the single layer appear like two layers, yielding an average of 1.5 layers. This explanation seems unlikely, however, in view of the data on thickness of the first layer.

The "subsidiary line" hypothesis would predict a subsidiary inflection or plateau in the cumulative percent of first layers in relation to thickness, and such is not apparent (Figure 4).

We found no correlation between thickness of the innermost growth layer and month of capture (Table 3). It is apparent from the data that the layers are formed rapidly (very few relatively thin innermost layers are seen) and probably throughout the year in the population.

With no basis for direct calibration, we provisionally use three alternative hypotheses of rate of layer deposition (similar to those put forth for the spotted dolphin, *S. attenuata*—Perrin et al. 1976) in the age-based analyses below, namely:

I. One and one-half layers per year, or

TABLE 3.—Thickness of innermost growth layer in teeth of 331 eastern spinner dolphins, with 3-12 layers, by month of capture.

Month	Sample size (no.)	Thickness of innermost layer = thickness of next youngest layer		
		Average (%)	Minimum (%)	Maximum (%)
Jan.	38	90.1	65	100
Feb.	107	83.3	20	100
Mar.	42	88.3	30	100
Apr.	13	81.1	50	100
May	9	89.9	67	100
Aug.	3	98.0	94	100
Oct.	7	71.1	47	100
Nov.	26	83.6	44	100
Dec.	5	94.0	73	91

- II. One and one-half layers in the first year and one per year thereafter, or
- III. One and one-half layers per year until puberty (at about nine layers in males and five to six layers in females) and one per year thereafter.

There is a rapidly increasing body of evidence (Perrin et al. 1976; Best 1976) that most delphinids accumulate growth layers at the rate of 1/yr, making Hypothesis II the most likely true of the three, but some uncertainty still exists, especially for tropical forms. We therefore express the conclusions of all age-based analyses below in terms of the three hypotheses. Other, more complex hypotheses can be suggested, but these three in our view probably include the truth.

Reproduction

The Male

Spermatogenesis is histologically evident in 50% of (right) testes weighing 94 g or more (weight of epididymis included) (Figure 17). A perhaps better criterion of sexual maturity is presence of sperm in the epididymis (Figure 18). Combined testis-epididymis weight at which half the males possess "some" or "copious" sperm in the epididymis is approximately 150 g. Another epididymal criterion can be defined, namely, the testis-epididymis weight above which the proportion of males having "copious" sperm in the epididymis does not increase, in this case above 50% at about 400 g. The three testis-epididymis weight criteria of 94 g (50% spermatogenic), 150 g (50% with

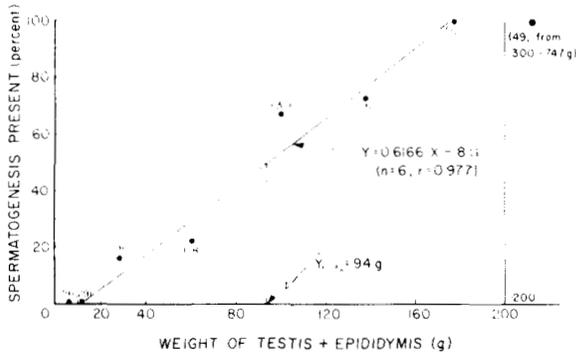


FIGURE 17.—Linear regression analysis of relationship between proportion of males spermatogenic and testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

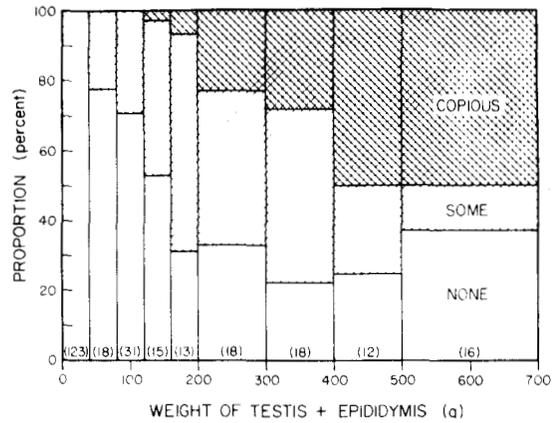


FIGURE 18.—Presence of sperm in epididymis in relation to testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

sperm in epididymis), and 400 g (asymptotic weight with respect to proportion with copious sperm) are considered below in relation to body length and age (in dentinal growth layers).

Testis-epididymis weight on the average increases precipitously with body length between 160 and 170 cm (Figure 19), but is only weakly correlated with body length beyond 175 cm. Males of any length above 160 cm can be mature or immature under each of the three criteria defined above. The proportion of males mature under the three criteria stabilizes at about 170 to 175, 175 to 180, and 180 to 185 cm body length, respectively (Figure 20). The average length of adult males under the three criteria ranges from 174 to 176 cm (Table 4).

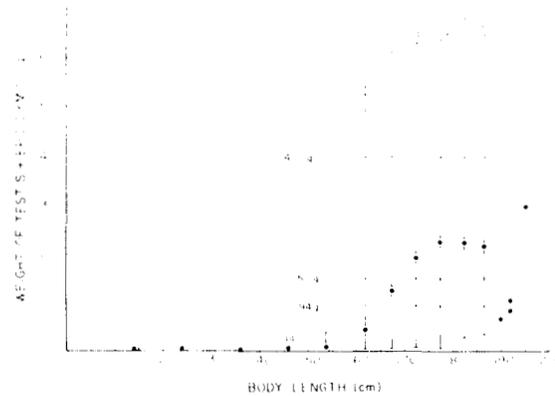


FIGURE 19.—Relationship between testis-epididymis weight and body length in the eastern spinner dolphin. Circled dots are sample means. Vertical bars are ranges. Sample sizes in parentheses.

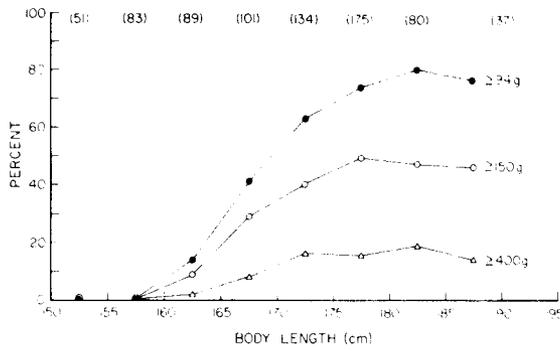


FIGURE 20.—Proportion of males sexually mature in relation to body length in the eastern spinner dolphin under three criteria of testis-epididymis weight. Sample sizes in parentheses.

TABLE 4.—Body length of adult male eastern spinner dolphins under three criteria of sexual maturity.

Weight of testis and epididymis (g)	Sample size (no.)	Body length (cm)			SD
		Minimum	Maximum	Average	
<94	594	108	192	—	—
≥94	356	160	195	176.0	5.99
≥150	230	160	195	175.8	6.06
≥400	81	162	190	174.1	5.79

Testis-epididymis weight is more closely correlated with age (in dentinal growth layers) than with body length (Figure 21). The 94-g level is reached on the average at about 9 growth layers and attained by all males with more than 12 layers. The 150-g level is reached at about 10 layers on the average and by all males at about 13 layers. The 400-g level is reached on the average at about 12 layers, but the oldest male examined (16.5 layers) had a testis-epididymis weight of only 333 g. Estimated average age in years at sexual maturity under the three criteria and under the three layer/year hypotheses ranges from 6.0 to 11.5 yr (Table 5), with the most likely estimates (Hypothesis II) 8.5 to 11.5 yr.

The question of age at attainment of social maturity (sense of Best 1969) in the spinner dolphin must await studies of social structure and breeding patterns. Other (larger) odontocetes, such as the sperm whale, *Physeter catodon*, and the long-finned pilot whale, *Globicephala melana*, are known or thought to be polygynous, to varying degrees, but the social structure of the spinner dolphin is as yet unknown.

No systematic seasonal variation in testis weight or condition was detected, although the heavy bias in seasonal coverage of the sample precludes an adequate evaluation of this factor.

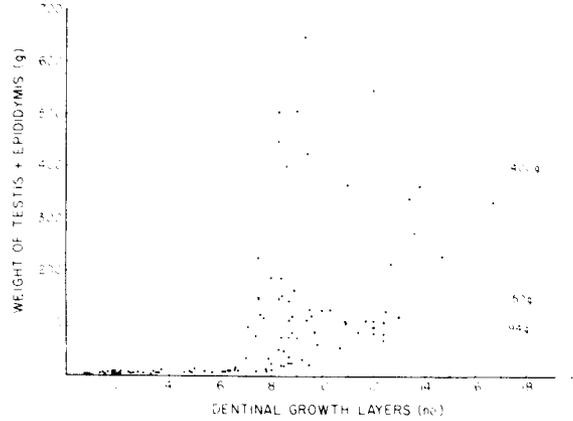


FIGURE 21.—Scatterplot of testis-epididymis weight on age (in dentinal growth layers) for 106 eastern spinner dolphins.

TABLE 5.—Estimated average age in years at attainment of sexual maturity in male eastern spinner dolphins under three criteria of maturity and three growth layer hypotheses. [See text for definition.]

Testis-epididymis criterion (g)	Age (years) under growth layer hypotheses		
	I	II	III
94	6.0	8.5	6.0
150	6.7	9.5	7.0
400	8.0	11.5	9.0

The Female

ATTAINMENT OF SEXUAL MATURITY. — The smallest sexually mature female in the present sample was 152 cm long. The largest immature female was 182 cm long. One estimate of average length at attainment of sexual maturity is the length at which 50% of the females show evidence of having ovulated, i.e. possess ovaries with one or more scars (corpus luteum or corpus albicans). This length in the present sample of eastern spinner dolphins is estimated at 164.1 cm (Figure 22).

The sigmoid curve in Figure 22 is slightly asymmetrical, that is to say, there are more immature animals (91) above the 50% -mature length of 164.1 cm than there are mature animals below it (62). At 165 cm, the numbers are 80 and 77, respectively. This length, 165 cm, is used below to classify as sexually mature or immature specimens for which ovarian data are lacking. The predicted number of growth zones (from the growth equation) at this length is 5.5.

Average age at attainment of sexual maturity can also be estimated directly from the smaller sample of females for which teeth were sectioned ($n = 247$). This analysis (Figure 23) estimates

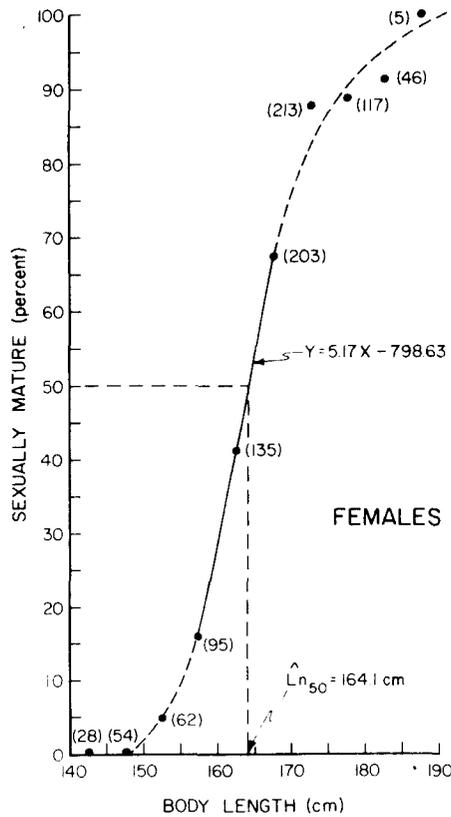


FIGURE 22.—Estimation of body length at which 50% of female eastern spinner dolphins show ovarian evidence of sexual maturity (one or more scars). Fit to central portion of curve (solid line) is linear regression. Dashed portions of curve fitted by eye. Sample sizes in parentheses.

average age at attainment of maturity at about 5.4 growth layers, in close agreement with the estimate derived from the age/length equation. A rounded-off average of 5.5 layers is used below. Average age in years at attainment of maturity under the three hypotheses of layer deposition rate are 3.7, 5.0, and 3.7 yr, respectively, with the second estimate being most probably correct.

Sexually adult females in the sample ranged from 152 to 187 cm and averaged 171.2 cm in length (Figure 24).

DISTRIBUTION OF CORPORA TO LEFT AND RIGHT OVARIES.—As in all other odontocetes so far studied, the left ovary predominates in ovulation. As in the case of *S. attenuata*, the distribution between left and right side (Table 6) can be accounted for by assuming that about 90 to 95% of the females ovulate the first time from the left ovary, and the remainder from the right, and that

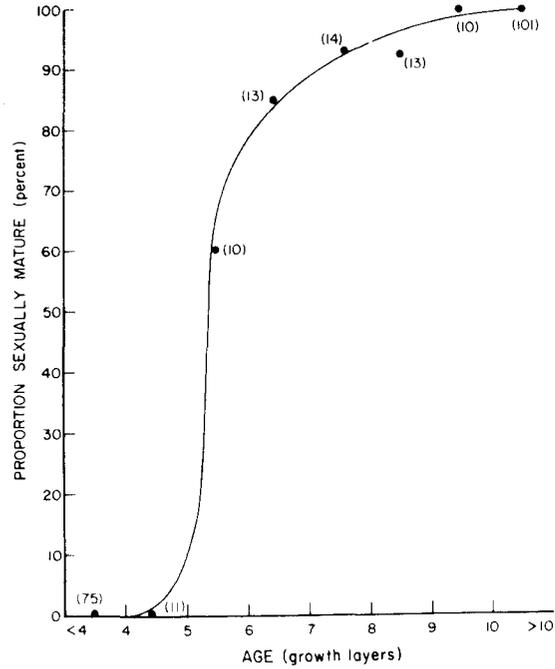


FIGURE 23.—Relationship between proportion of females sexually mature and age, in dentinal growth layers, in the eastern spinner dolphin. Fit is by eye.

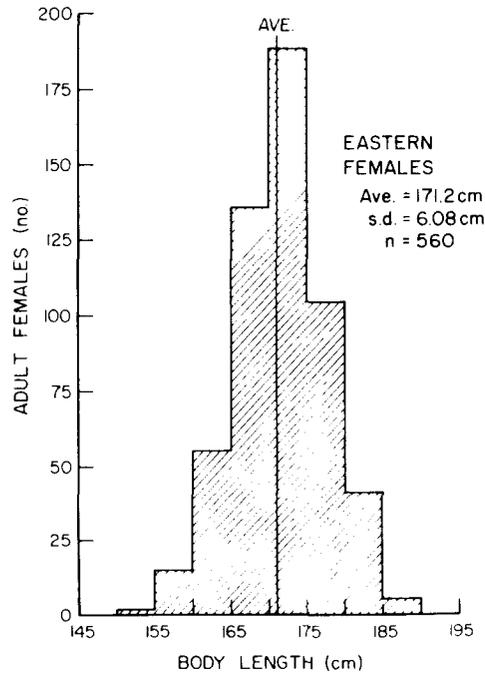


FIGURE 24.—Length-frequency distribution of 560 sexually adult (possessing at least one ovarian corpus) female eastern spinner dolphins.

TABLE 6.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 556 eastern spinner dolphins.

Corpora (no.)	Sample size (no.)	Location of corpora		
		Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	41	92.7	7.3	—
2	51	78.4	9.8	11.8
3	50	92.0	2.0	6.0
4	43	90.7	2.3	7.0
5	56	91.1	3.6	5.3
6	53	86.8	11.3	1.9
7	60	85.0	15.0	0.0
8	39	82.1	10.3	7.6
9	26	80.8	11.5	7.7
10-11	63	73.0	19.0	8.0
12-15	55	41.8	1.8	56.4
16-19	13	23.1	0.0	76.9
20-26	6	16.7	0.0	83.3

succeeding ovulations are from the same ovary (left or right) about 90 to 95% of the time. When about 10 corpora have accumulated, emphasis shifts sharply to the opposite ovary.

OVULATION RATE.—The number of ovarian corpora, including corpora lutea, ranged from 1 to 26 in 555 sexually adult females. The frequency distribution (Figure 25) is very similar in shape to that for *S. attenuata* (Perrin et al. 1976) with highest frequencies at 5 to 7 corpora and a sharp falloff after about 10 corpora.

Size-frequency distribution of the various types of corpora albicantia among the corpora-type categories relative to total number of corpora were the same in this sample as in the sample of *S. attenuata* previously studied (Perrin et al. 1976)

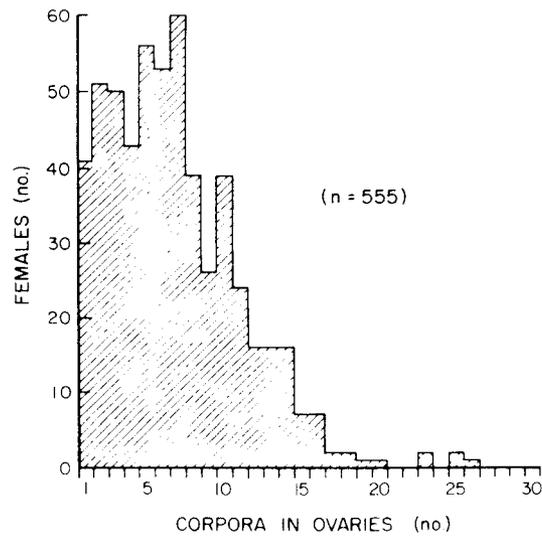


FIGURE 25.—Frequency distribution of ovarian corpora count in 555 female eastern spinner dolphins.

leading us to believe that, for this species also, corpora of ovulation persist throughout the life of the animal, accumulating at Type 3.

Scatter in a plot of number of corpora on age in growth layers is wide (Figure 26) but not as great as encountered in a study of *S. attenuata* (Perrin et al. 1976). Factors producing the scatter are 1) error in reading growth layers, 2) individual variation in ovulation rate, and 3) change in ovulation rate during the reproductive span. The teeth of *S. longirostris* in this study had more clearly defined, more easily readable growth layers than did those of *S. attenuata* in the previous study, and this probably accounts for the relatively less scatter for the former, although less influence by either or both of the other two factors cannot be ruled out.

Calculation of average ovulation rates from the data in Figure 26 must take into account individual variation in age at first ovulation. The data were grouped into 2-layer intervals (all those with 12 or more layers were included in a single final increment), and average reproductive age by interval *P* calculated as

$$\bar{A} = \frac{\sum_{i=1}^P a_i b_i}{c_i}$$

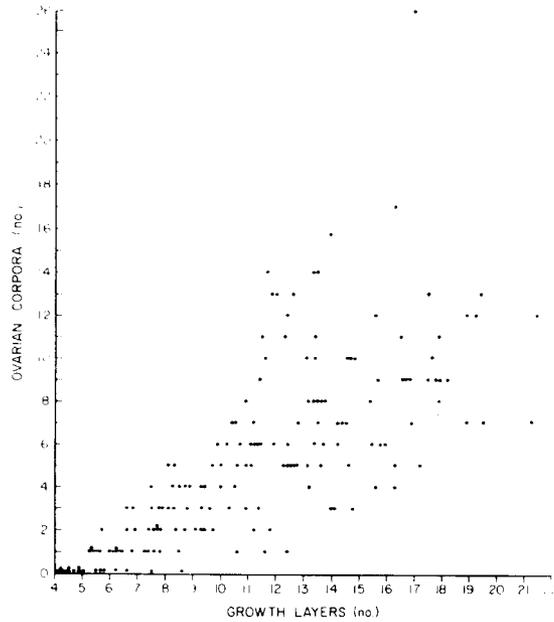


FIGURE 26.—Scatterplot of number of ovarian corpora on age in dentinal growth layers, in 1,972 female eastern spinner dolphins.

where a_i = percent maturing in i th interval (percent maturing in i minus percent maturing in $i - 1$)

b_i = average reproductive age in interval P of females maturing in i

c_i = percent mature in interval P .

Average reproductive age in the i th interval of females maturing in i was set at 0.50 layer. A plot of number of ovulations on average reproductive age (Figure 27) shows linear increase, with a slope of unity (one ovulation per layer), in number of corpora until about 10 layers of reproductive age (15.5 layers total age on the average) when the ovulation rate apparently drops sharply. This is very different from the results obtained in a similar best-fit analysis for *S. attenuata* (Perrin et al. 1976), which indicated average ovulation rates of about four during the first layer, two during the second, and about one per layer thereafter. A power fit to the data for *S. longirostris* (Figure 27) shows much less variation in ovulation rate with age. It appears that in the presently sampled population of *S. longirostris* there is less multiple infertile ovulation in very young mature females than in the studied population of *S. attenuata*. This may be an inherent difference or may reflect differential status of the two populations with respect to exploitation. For example, females could on the average become sexually mature at an earlier age

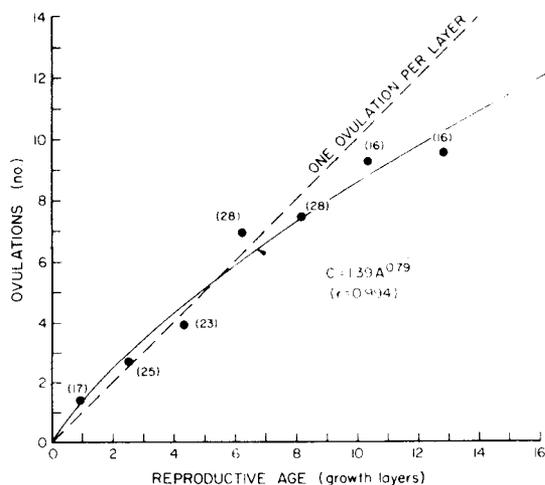


FIGURE 27.—Scatterplot of 2-layer means (last mean is for 12-16 layers) of average number of ovulations on average reproductive age in growth layers in the eastern spinner dolphin. Regression line is power fit. One-ovulation-per-layer line added. Sample sizes in parentheses.

in an exploited population but be less fertile, in terms of pregnancies per ovulation, than had they become mature at greater age. Estimated ovulation rates were higher in the studied eastern Pacific population of *S. attenuata* than in a relatively unexploited population of the same species in Japanese waters (Perrin et al. 1976).

POSTREPRODUCTIVE FEMALES.—Four adult females of 536 examined ($\approx 1.0\%$) showed clear evidence of being postreproductive, or "senile," by criteria of 1) being inactive, or "resting" (neither pregnant nor lactating); 2) having high corpora count (≥ 10); 3) having small, withered ovaries (weighing < 3.5 g); 4) having no developing follicles (largest follicle < 1 mm in diameter); and 5) having no Type 1 or 2 corpora albicantia (terminology of Perrin et al. 1976), indicating recent ovarian activity (Figure 28).

THE CALVING CYCLE AND PREGNANCY RATE.—The calving cycle, for purposes of analyzing the types of field data available, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting"—a catch-all "phase" for animals neither pregnant nor lactating, which includes

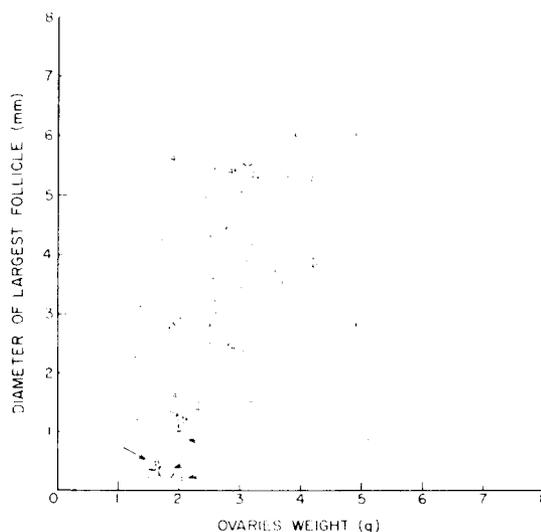


FIGURE 28.—Scatterplot of diameter of largest follicle on combined weight of ovaries for 73 adult female eastern spinner dolphins classified as "resting" (not pregnant or lactating). Specimens with corpora lutea or cystic follicles not included. Number in circle is total number of corpora in ovaries (including corpus luteum). Double circles are specimens with no Types 1 or 2 corpora albicantia indicating recent ovarian activity. Four postreproductive females indicated with arrows.

females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf.

The gestation phase of the cycle was estimated above, at 10.6 mo. We estimated average length of lactation by two methods: 1) by assuming that the proportion of a sample of mature females in a particular reproductive phase is directly proportional to the relative length of that phase in the overall cycle, i.e., that the samples are not biased with regard to reproductive phase (the length of the "resting" phase was also estimated this way); and 2) by assuming that a suckling calf exists for each lactating female, and the samples are unbiased with respect to suckling calves and lactating females, under which assumptions the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length (and, from the growth equation, age) at weaning. The first estimate was based on data for 536 adult females collected 1971-75, classified as pregnant, lactating, pregnant and lactating, "resting," or post-reproductive (Table 7). The resting females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). Only three females were simultaneously pregnant and lactating (1.44% of lactating females).

Subtraction of the postreproductive females and allocation of the females both pregnant and lactating to both of the two categories provides estimates of the proportions of the reproductive females in the three phases of the cycle (Figure 29) and of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, using the estimated gestation

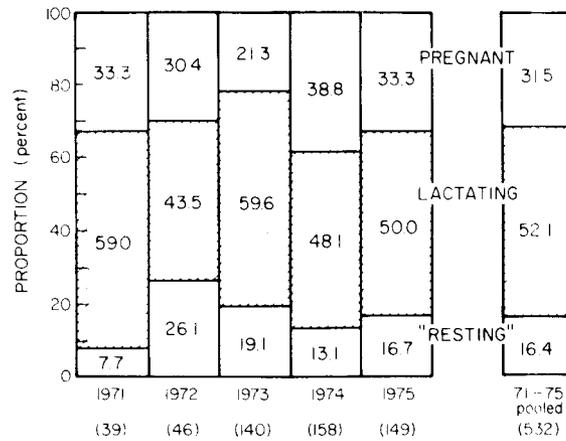


FIGURE 29.—Proportions of 532 adult reproductive female eastern spinner dolphins in pregnant, lactating, and "resting" (not pregnant or lactating) phases of cycle. Based on Table 4. Females both lactating and pregnant allotted to both phases. Postreproductive females excluded.

period of 10.6 mo (Method 1 in Table 8). The estimates of average length of lactation thus derived range from 13.1 to 29.7 mo (the possible causes of this wide year-to-year variation in phase structure of the samples are discussed below in Gross Annual Reproduction), with a pooled average of 17.5 mo.

The second method of estimating length of lactation, the "cumulative calf length/lactating females" method yielded estimates for six single-month samples ranging from 7.7 to 16.0 mo and for single-year samples from 9.4 to 10.6 mo (Method 2 in Table 8). The pooled estimate for 1973-75 is 10.1 mo. The three yearly estimates are consistent with each other and sharply lower than the estimates yielded by the "proportion-in-phase" method above (compare in Table 9). The first method could be invalid and cause disparate estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples, or conversely, 2) either (or both) pregnant or "resting" females were underrepresented. This situation could obtain if lactating females and their

TABLE 7.—Reproductive condition of 536 adult female eastern spinner dolphins collected 1971-75.

Condition	1971		1972		1973		1974		1975		1971-75 pooled	
	No.	%	No.	%								
Pregnant only	13	33.3	14	30.4	29	20.6	60	37.3	49	32.9	165	30.8
Lactating only	23	59.0	20	43.5	83	58.9	75	46.6	74	49.7	275	51.3
Pregnant and lactating	0	0	0	0	1	0.7	2	1.2	1	0.7	4	0.7
"Resting"												
with corpus luteum	0	0	4	8.7	3	2.1	5	3.1	3	2.0	15	2.8
without corpus luteum	3	7.7	8	17.4	24	17.0	16	9.9	22	14.8	73	13.6
Postreproductive	0	0	0	0	1	0.7	3	1.9	0	0	4	0.7
Total	39	100.0	46	100.0	141	100.0	161	100.0	149	100.0	536	100.0

TABLE 8.—Estimated lengths of postreproductive phases, under two methods of estimating length of lactation, of the eastern spinner dolphin based on single-year samples, 1971-75, and on pooled samples for all years, with estimates of pregnancy rate and calving interval based on lactation estimate 1.

Item	1971	1972	1973	1974	1975	Pooled
Sample size (no.)	39	46	140	158	149	532
Pregnancy (months)	10.6	10.6	10.6	10.6	10.6	10.6
Lactation (months):						
Method 1	18.8	15.2	29.7	13.1	15.9	17.5
Method 2 (Hyp. II)	—	—	10.6	9.4	10.2	10.1 (1973-75)
"Resting" (Method 1)	2.6	9.1	9.5	3.6	5.3	5.5
Sum of phases:						
Method 1 (months)	32.0	34.9	49.8	27.4	31.8	33.6
Method 1 (years)	2.66	2.91	4.15	2.28	2.65	2.80
Method 2 (months)	—	—	26.7	25.5	26.3	26.2
Method 2 (years)	—	—	2.23	2.13	2.19	2.18
Annual pregnancy rate (APR):						
Method 1	0.375	0.344	0.243	0.444	0.380	0.360
Method 2	—	—	0.450	0.474	0.459	0.461
Calving interval (1/APR):						
Method 1 (years)	2.66	2.91	4.12	2.25	2.63	2.78
Method 1 (months)	32.0	34.9	49.5	27.0	31.6	33.4
Method 2 (years)	—	—	2.22	2.11	2.18	2.17
Method 2 (months)	—	—	26.6	25.3	26.2	26.1

TABLE 9.—Estimates of length of lactation in the eastern spinner dolphin based on the "cumulative calf length/lactating females" method (see text), for 6 single-month samples and for 1973-75 by year and pooled.

Sample	Lactating females ¹ (no.)	Length at which cumulative number of calves = number of lactating females (cm)	Length of lactation (months, under Hypotheses)		
			I	II and III	Layers
Feb. 1973	41	139	1.83	14.6	16.0
Mar. 1973	18	133	1.52	12.2	12.2
Jan. 1974	23	124	1.16	9.3	9.3
Feb. 1974	42	118	0.97	7.7	7.7
Jan. 1975	33	132	1.48	9.4	9.4
Feb. 1975	12	120	1.03	8.2	8.2
Year:					
1973	91	128.5	1.33	10.6	10.6
1974	81	124.5	1.18	9.4	9.4
1975	88	127.0	1.27	10.2	10.2
Pooled	260	126.7	1.26	10.1	10.1

¹Includes mature females (>165 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.

accompanying calves are more likely to be captured and killed in the net because of limitations imposed on endurance of the mother by that of the calf, certainly lower than adult endurance. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples, or, conversely, 2) lactating females were underrepresented. Recent data for *S. attenuata* (J. E. Powers pers. commun.) indicate that small calves are probably overrepresented in small single-set samples of that species. This may be caused by the above-mentioned lesser stamina of calves in the energetically stressful purse seine chase, capture, and release sequence. The lesser year-to-year variation in the estimates yielded by Method 2 also supports the idea that these may be

better estimates. If neonates are overrepresented in the samples, however, then the percent pregnant must be underestimated to some unknown, but small, degree. In view of these considerations, both the proportion-in-phase estimate and the cumulative calf length/lactating female estimate are used below as alternatives in estimating pregnancy rate, calving interval, and gross annual reproduction, and we conclude that the true length of lactation in an unperturbed birth-to-weaning period can be assumed to lie somewhere between the estimates yielded by the two methods.

Annual pregnancy rate by Method 1 was calculated by division of the proportion pregnant (Figure 29) by the length of gestation (0.875 yr). The reciprocal of annual pregnancy rate is the esti-

estimate of average calving interval. For the Method 2 estimates, calving interval was calculated by summing the phases, taking into consideration overlapping cycles by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant. Lacking an independent estimate of the length of the "resting" phase, the Method 1 estimate for 1973-75 was used as a reasonable approximation in the Method 2 calculations of length of cycle and calving interval.

CHANGES IN REPRODUCTIVE RATES WITH AGE.—Pregnancy rate in the sample decreases with age after about 12 layers (8.0, 11.5, or 10.2 yr, depending upon whether layer Hypothesis I, II, or III is applied, respectively), while lactation rate rises (Figure 30). Assuming that the samples are representative of the population, this may mean that 1) pregnancy rate decreases with age in the individual, or 2) that older females belong to older cohorts in which reproductive rates have been lower than in younger cohorts since recruitment to the breeding population. The former seems most likely; it would appear that older females have fewer calves and nurse them longer. The same result was obtained for *S. attenuata* in the eastern Pacific (Perrin et al. 1976).

Sex Ratios

Sex ratios are at or very near parity at birth and overall in the samples (Table 10), but there were slightly more females than males in adults in the samples for each of the 3 yr 1973-75, a result consistent with that encountered in *S. attenuata* (Perrin et al. 1976) but less pronounced.

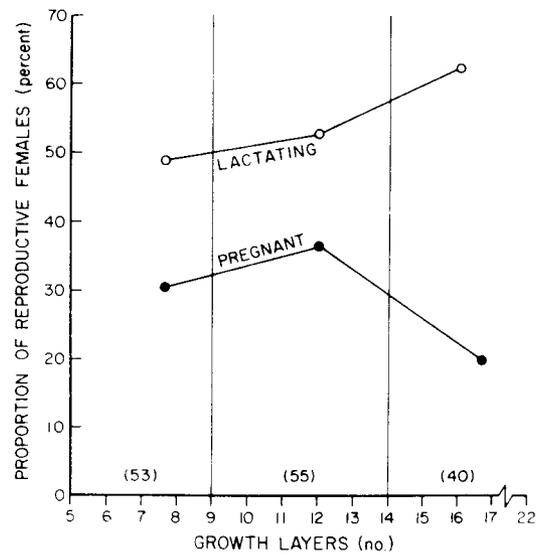


FIGURE 30.—Change in reproductive rates with age in the eastern spinner dolphin. Sample sizes in parentheses.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be made based on 1973-75 samples, the 3 yr for which the samples are large and nonselected with respect to age and sex structures (Table 11). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then the proportion of total females which are reproductive and pregnancy rate (for Method 1) are underestimated and the proportion of total sample female is overestimated, all to an unknown, but probably small, degree. Standard er-

TABLE 10.—Sex ratios in 126 fetuses and 2,261 neonatal-to-adult eastern spinner dolphins. Fetal samples limited to fetuses longer than 15 cm.

Stage	Length (cm)	Sample size (no.)	Average length (cm)	Females		Males		Sex ratio (M = F)
				No.	%	No.	%	
Fetuses	15	126	49.0	65	51.6	61	48.4	0.94
Neonates to adults	70-129	294	116.0	140	47.6	154	52.4	1.10
	130-149	269	141.2	132	49.1	137	50.9	1.04
	150-159	362	154.9	186	51.4	176	48.6	0.95
	160							
	(adult size):							
	1973	408	171.2	207	50.7	201	49.3	0.97
	1974	439	171.3	226	51.5	213	48.5	0.94
	1975	483	172.4	254	52.6	229	47.4	0.90
	1973-75 pooled	1,330	171.7	687	51.7	643	48.3	0.94
	Total: ¹							
	1973	688	—	342	49.7	346	50.3	1.01
	1974	797	—	395	49.6	402	50.4	1.02
	1975	776	—	411	53.0	365	47.0	0.89
	1973-75 pooled	2,261	—	1,148	50.8	1,113	49.2	0.97

¹Includes six specimens for which length data not available.

TABLE 11.—Calculation of estimates of gross annual reproductive rate of the eastern spinner dolphin, 1973-75. Standard error follows estimate (see text). Sample sizes in parentheses.

Year	A	B	C		A × B × C	
	Proportion female	Proportion of females reproductive	Annual pregnancy rate		Gross annual reproductive rate	
			Method 1	Method 2	Method 1	Method 2
1973	0.497 ± 0.019 (690)	0.443 ± 0.027 (343)	0.243 ± 0.036 (140)	0.450 ± 0.042 (140)	0.054 ± 0.009 (690)	0.099 ± 0.011 (690)
1974	0.496 ± 0.018 (797)	0.438 ± 0.025 (391)	0.444 ± 0.040 (158)	0.474 ± 0.042 (158)	0.096 ± 0.010 (797)	0.103 ± 0.011 (797)
1975	0.530 ± 0.018 (776)	0.432 ± 0.024 (410)	0.380 ± 0.040 (149)	0.459 ± 0.041 (149)	0.087 ± 0.010 (776)	0.105 ± 0.011 (776)
1973-75 pooled	0.508 ± 0.011 (2,262)	0.437 ± 0.015 (1,144)	0.360 ± 0.028 (447)	0.461 ± 0.024 (447)	0.080 ± 0.006 (2,262)	0.102 ± 0.006 (2,262)

rors (SE) are attached to the various estimates where sample size ≥ 100, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of SE as:

$$SE = \sqrt{p(1-p)/n}$$

Although gross annual reproductive rate as calculated in Table 11 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), allowing estimation of the variance by the above method. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The only statistically significant differences among the estimates year-to-year (at α = 0.05) are between the Method 1 estimates for 1973 and 1974 of annual pregnancy rate and, as a result of that, gross annual reproductive rate. This sharp and real shift cannot be accounted for by a time-sampling effect, because seasonal coverage in the 2 yr was approximately the same. Prompted by the knowledge that areal variation may exist in the timing of calving peaks and/or in the degree of breeding synchrony (see Length of Gestation and Fetal Growth), we divided the data for each of the years into three geographical strata: an "inside" sample, an "outside" sample, and a "southern sample" (Figure 31). More of the 1973 sample was taken from the outside area than from the inside area (108 versus 28), and the reverse was true in 1974 (46 versus 106). The southern samples, 5 in 1973 and 14 in 1974, were too small for analysis. Comparison of the distribution of reproductive condition in inside and outside samples in 1973 and 1974, however, reveals very small areal differences compared with those between years (Table 12). It must be concluded that the sharp in-

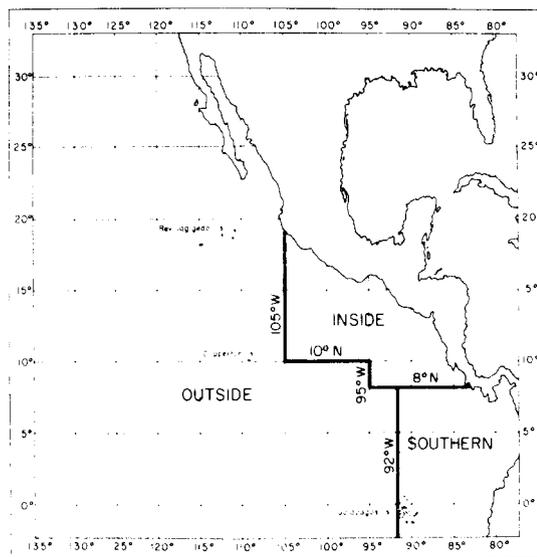


FIGURE 31.—Areas used to stratify 1973-74 samples of distribution of reproductive condition in female eastern spinner dolphins.

TABLE 12.—Distribution of reproductive condition in area-stratified samples of sexually adult female eastern spinner dolphins in 1973 and 1974.

Year	Inside	Outside
	(n = 134)	(n = 154)
1973	(n = 28)	(n = 108)
(n = 136)	14.3% pregnant	19.4% pregnant
	57.1% lactating	61.1% lactating
	3.6% pregnant and lactating	0.0% pregnant and lactating
	25.0% "resting"	18.5% "resting"
	0.0% postreproductive	0.9% postreproductive
1974	(n = 106)	(n = 46)
(n = 152)	38.7% pregnant	39.1% pregnant
	48.1% lactating	50.0% lactating
	0.0% pregnant and lactating	4.3% pregnant and lactating
	10.4% resting	6.5% resting
	2.8% postreproductive	0.0% postreproductive

crease in percent pregnant and decrease in percent lactating from 1973 to 1974 is not a seasonal or areal effect. Several other possible explanations exist, to wit:

- 1) The samples were biased with respect to reproductive structure of the population, in one or both years or differently in the 2 yr.
- 2) The change was a real and normal event, perhaps reflecting differential breeding rates in single-year cohorts (the data suggest about a 3-yr cycle—see below—and the 1974 rates were similar to those for 1971).
- 3) An anomalous increase in pregnancy rate occurred from 1973 to 1974, perhaps related to exploitation in the tuna fishery or to natural variation in the pelagic environment.

The balance of evidence discussed above favors the first alternative, suggesting that the Method 2 estimates of gross annual reproduction are the more accurate of the two alternative sets of estimates.

DISCUSSION

Comparison with the Spotted Dolphin

The estimated gross reproductive rates (Method 1) for the eastern spinner dolphin are lower than those estimated for the offshore spotted dolphin by Perrin et al. (1976), 10 to 11%, as opposed to 14%. Three major points of difference between the data for the two species contribute to this disparity.

- 1) A higher proportion of the spotted dolphins were females (55.1% as opposed to 50.8% in the present 1973–75 sample of eastern spinner dolphins).
- 2) The proportion of total females which were reproductive was higher for the spotted dolphin (55.7% as opposed to 43.7% for the eastern spinner dolphin).
- 3) There is apparently much less overlapping of reproductive cycles in the eastern spinner dolphin than in the spotted dolphin in the eastern Pacific. Only 1.4% of lactating females examined were simultaneously pregnant, as opposed to 9.6% in the spotted dolphin, a seven-fold difference. At least part of this difference may be inherent in the species; the rate in the unexploited western Pacific population of spotted dolphin is 5.1% (Kasuya et al. 1974), still nearly four times greater than in the eastern spinner dolphin.

In summary, the data suggest that there is an inherent difference in reproductive capability be-

tween the spotted and spinner dolphins, but that part of the total difference in present reproductive rate may be related to differential exploitation. Gross annual reproductive rate in the unexploited western Pacific population of *S. attenuata* is estimated at 0.094 (calculated from data in Kasuya et al. 1974—0.57 female \times 0.61 mature \times 0.27 annual pregnancy rate = 0.094/yr), as opposed to 0.144 in the exploited eastern Pacific population of the same species, a possible example of difference in rate correlated with differential exploitation. Whereas the western Pacific population is thought to be virtually unexploited and at its original size, the eastern Pacific population is estimated to be at 62% of its original, preexploitation size (midpoint estimate).⁸

Comparison with Other Cetaceans

The estimates of gross annual reproductive rate for the eastern spinner dolphin lie at the lower end

⁸Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. SWFC Admin. Rep. LJ-76-29, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 109 p. (Unpubl. rep.)

TABLE 13.—Estimated gross annual reproductive rate of the eastern spinner dolphin compared with estimated rates for other cetaceans. Data for *S. attenuata* from Perrin et al. (1976) for eastern Pacific and Kasuya et al. (1974) for western Pacific; for *S. coeruleoalba* from Kasuya (1972), for *Delphinus* from Danilevskiy and Tyutyunnikov (1968); for *Globicephala* from Sergeant (1962); for *Delphinapterus* from Sergeant (1973); and for *Eschrichtius* from Rice and Wolman (1971). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975); alternative common name in parentheses.

Species and locality	Exploited (now or in past)	Gross annual reproductive rate
Eastern spinner dolphin (porpoise), <i>Stenella longirostris</i> subsp. <i>S. attenuata</i>	Yes	0.08 (pooled 1973-75)
Spotted dolphin (porpoise), <i>S. attenuata</i>		
Eastern Pacific	Yes	0.14
Western Pacific	No	0.09
Striped dolphin (streaker porpoise), <i>S. coeruleoalba</i> , in western Pacific	Yes	0.11
Common dolphin (whitebelly porpoise), <i>Delphinus delphis</i> , in Black Sea	Yes	0.14
Long-finned pilot whale (pot-head whale), <i>Globicephala melaena</i> , in western North Atlantic	Yes	0.10 to 0.13
White whale (beluga), <i>Delphinapterus leucas</i> , in western Hudson Bay	Yes	0.12
Gray whale, <i>Eschrichtius robustus</i> , in eastern North Pacific	Yes	0.13

of the range of estimates for other cetaceans (Table 13), with only the estimate for 1974 included in the range. The estimated rates for populations thought to have declined due to exploitation (*S. attenuata* in the eastern Pacific—Perrin et al. 1976; *D. delphis* in the Black Sea—Danilevskiy and Tyutyunnikov 1968; and *Eschrichtius*—Rice and Wolman 1971) are very close to each other, at 13 or 14%.

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